

Decline and Recovery of Atlantic Cod (*Gadus morhua*) Stocks throughout the North Atlantic

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Abstract

Many stocks of Atlantic cod (*Gadus morhua*) on both sides of the North Atlantic are currently at much reduced levels of biomass, but this situation is not in all instances the result of long, continuous decline. Most Northwest Atlantic stocks declined to low levels during the 1970s, but increased during the 1980s before declining even more severely during the late 1980s and early 1990s. Several of these stocks have shown little recovery despite severe restrictions on directed fishing. Many stocks in the Northeast Atlantic have experienced sustained increases and sustained decreases, but generally not in concert. Among-stock comparisons illustrate that fishing has played a dominant role in the dynamics of all cod stocks, but variability in climate has contributed to variability in recruitment, individual growth, and natural mortality. A cooling event during the last three decades of the twentieth century contributed to the rapid decline of several stocks in the Northwest Atlantic, and changes in life-history traits (growth rate, age and size at maturity) and in the biotic environment (predators and prey) may be contributing to recovery being slow.

Introduction

The Atlantic cod (*Gadus morhua*) is distributed in an arc across the North Atlantic. Stocks are recognized for management purposes from Georges Bank northward to Labrador, then northeastward to West and East Greenland, Iceland, and the Barents Sea (arcto-Norwegian or north-

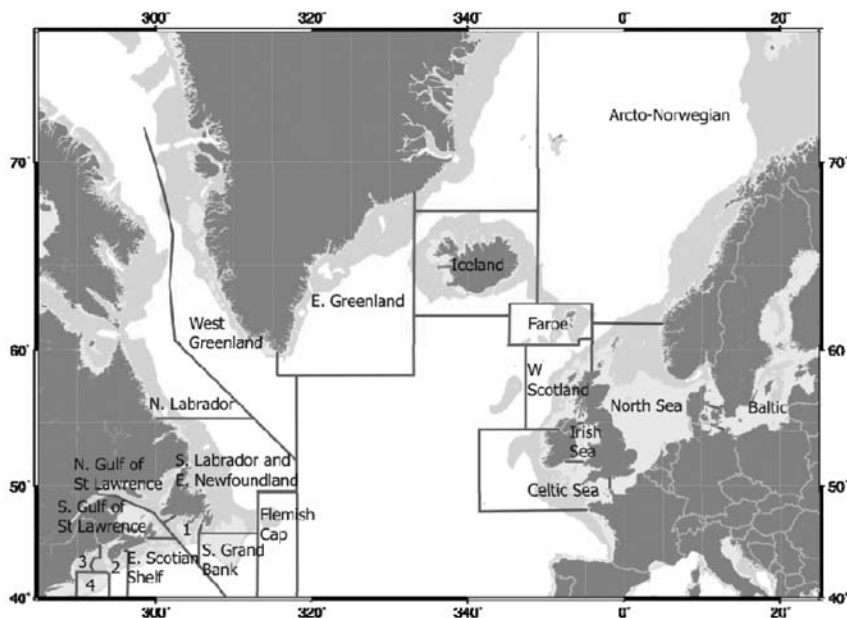


Figure 1. Map of the North Atlantic, showing the location of cod stocks. The stocks represented by numbers are 1 = S. Newfoundland, 2 = W. Scotian Shelf, 3 = Gulf of Maine, and 4 = Georges Bank. The map does not extend sufficiently to the southwest to include the whole of the Georges Bank stock area, nor does it extend sufficiently to the northeast to encompass the full range of the arcto-Norwegian stock in the Barents Sea. The boundaries of the Kattegat, West Baltic, and East Baltic stocks are not illustrated.

east arctic cod), and then southward to the Celtic Sea and eastward to the Baltic Sea (Fig. 1). All stocks are currently below the maximum biomass experienced during the past few decades, and most are at much lower levels (Brander 2007). However, these low levels are generally not the result of a long, steady decline. Most stocks in the Northwest Atlantic share a common pattern of a marked decline during the 1970s, an increase during the 1980s, and a severe decline during the late 1980s and early 1990s. Several of these stocks have shown little or no recovery during the past decade despite severe reduction or even cessation of directed fishing (Shelton et al. 2006). In contrast to the Northwest Atlantic stocks, the prolonged increases and decreases experienced by many stocks in the Northeast Atlantic tend not to be temporally correlated, and the declines have been less severe (Brander 2007). Many cod

stocks on both sides of the Atlantic have also experienced changes in demographic properties, such as age/size composition and geographic substructure, and changes in life-history traits, such as age and size at maturity and growth rate. While fishing has played a dominant role in the dynamics of most of these stocks, it is clear that changes in the environment have contributed to changes in recruitment, growth, and natural mortality. Comparisons among stocks may help clarify the relative roles of changes in fishing pressure, the physical environment, and the biotic environment in terms of both predators and prey. We report some of the findings of a workshop (ICES 2006b) that reviewed and synthesized knowledge regarding factors influencing the decline and recovery of cod stocks. Particular attention is given to reasons for non-recovery of several of the Northwest Atlantic stocks.

Atlantic cod stocks

Cod stocks differ in many respects. Some (e.g., southern Grand Bank, Flemish Cap) are associated with shelf areas far from land, but most stocks inhabit areas adjacent to a land mass. Some of the latter stocks have components associated with the coast, and these may be relatively distinct and sedentary, especially if they inhabit fjord systems such as at West Greenland (Hovgård and Wieland 2008) and Norway (Løken et al. 1994). Many such “unit stocks” are considered to represent stock complexes or metapopulations (Smedbol and Wroblewski 2002, Horwood et al. 2006).

The ecosystems in which the stocks are embedded differ in many aspects. For example, temperature decreases from south to north on both sides of the North Atlantic, but the difference in temperature between east and west at a given latitude can be substantial because of the pattern of ocean circulation. The Labrador Current and local winter cooling produce low temperatures off Labrador and eastern Newfoundland, in the Gulf of St. Lawrence, and on the eastern Scotian Shelf, whereas the North Atlantic Drift warms the coasts of Europe and provides suitable temperature conditions for cod far into the Barents Sea. Average bottom temperatures, as reported by Brander (2007), vary from 0°C off Labrador to 11°C in the Celtic Sea.

The ecosystems also vary with respect to finfish diversity. The arcto-boreal ecosystems (Labrador-Newfoundland, Iceland, Barents Sea) have historically been dominated by one piscivorous fish species (cod) and one forage species (capelin, *Mallotus villosus*) (Livingston and Tjelmeland 2000). In contrast, ecosystems toward the southern limit of the cod's distribution, such as Georges Bank in the west and the North Sea in the east, have a broader array of piscivores and potential prey. The Baltic Sea fauna is depauperate compared to the adjacent North Sea because of its low salinity, and has historically been dominated by cod and two species of clupeoids serving as forage fish.

The stocks have historically differed considerably in size (Table 1; Fig. 2). During the period for which data are available, the maximum biomass of both the West Greenland and arcto-Norwegian cod has been estimated at about 4 million t immediately after the Second World War, whereas another four (S. Labrador–E. Newfoundland in the northwest and Iceland, North Sea, and eastern Baltic Sea in the northeast) have exceeded 1 million t. In contrast, the Gulf of Maine stock in the northwest and the west Scotland, Irish Sea, and Celtic Sea stocks in the northeast have not exceeded 60,000 t.

Changes in total biomass

Information on population dynamics is available for most stocks from mathematical reconstruction models (sequential population analysis, SPA) that are based on commercial catch data and biological sampling of size and age distributions as well as on fishery-independent indices of abundance (ICES 2005, Shelton et al. 2006, Brander 2007). (We use SPA as a generic term for such models, which include virtual population analysis, VPA.) It is common in inter-stock comparisons to focus on trends in spawning stock biomass (SSB) (e.g., Myers et al. 1996) because of the implicit, though flawed (Marteinsdottir and Begg 2002), assumption of proportionality between SSB and reproductive potential. However, trends in SSB may not reflect the extent of stock decline if the computation of SSB incorporates the decline in age-at-maturity documented for many stocks (Bratney et al. 2005). Therefore, we will focus on trends in total biomass (Table 1; Fig. 2).

Although the output of reconstruction models is a valuable source of information on the dynamics of individual stocks, models may differ greatly among stocks with respect to structure, assumptions, and the inclusion of data such as unreported catch, recreational catch, discards, and estimates of removals by conspecifics and other predators. The extent to which such differences influence the results of inter-stock comparisons is generally not documented. In addition, the time periods covered may differ considerably, which hampers the comparison of long-term trends. Some models go back to the 1940s and even beyond, but many go back only to the 1970s or even just the 1980s. In addition, SPA has been discontinued for formal assessment of some stocks (Table 1), viz. West Greenland (Hovgård and Wieland 2008), S. Labrador–E. Newfoundland (Lilly 2008), Flemish Cap (Vázquez and Cerviño 2005), eastern Scotian Shelf (Fanning et al. 2003), western Scotian Shelf (Clark and Hinze 2004) and, most recently, southern Newfoundland (DFO 2006). In most of these cases, the stock trajectories continue to be monitored by bottom-trawl surveys. For example, the survey of the S. Labrador–E. Newfoundland stock indicates that biomass in the offshore continued to decline after the decision that SPA models were no longer reflective

Table 1. Stock names, management areas, the period covered by recent population models and the maximum total biomass within that period.

Stock	NAFO or ICES management area	SPA period	Maximum total bio-mass (1,000 t) (year)	Data sources and ICES assessment working group codes
West Greenland (WGR)	1	1946-1989	4,129 (1949)	Buch et al. 1994; updated by Hovgård and Wieland 2008
N. Labrador (NLAB)	2GH	–	–	Lilly and Murphy 2004
S. Labrador–E. Newfoundland (SLEN)	2J3KL	1962-1992	2,982 (1962)	Bishop et al. 1993
Flemish Cap (FLEM)	3M	1972-2001	113 (1976)	Vázquez and Cerviño 2002
S. Grand Bank (SGBK)	3NO	1959-2004	395 (1967)	Power et al. 2005
S. Newfoundland (SNF)	3Ps	1977-2004	200 (1985)	Bratney et al. 2005
N. Gulf of St. Lawrence (NGSL)	3Pn4RS	1974-2005	603 (1983)	Fréchet et al. 2005
S. Gulf of St. Lawrence (SGSL)	4TVn	1971-2004	474 (1986)	Chouinard et al. 2006
E. Scotian Shelf (ESS)	4Vsw	1970-1997	320 (1985)	Mohn et al. 1998; Fanning et al. 2003
W. Scotian Shelf (WSS)	4X	1983-2002	77 (1983)	Clark et al. 2002; Clark and Hinze 2004
Gulf of Maine (GOM)	5Y	1982-2004	41 (1982)	Mayo and Col 2005
Georges Bank (GEOB)	5Z, 6	1978-2004	141 (1981)	O'Brien et al. 2005
Arcto-Norwegian (ARNO)	I, II	1946-2004	4,169 (1946)	ICES 2005; AFWG
Kattegat (KAT)	IIlc	1971-2004	45 (1973)	ICES 2005; WGBFAS
W. Baltic (WBAK)	IIId, 22-24	1970-2004	116 (1972)	ICES 2005; WGBFAS
E. Baltic (EBAL)	IIId, 25-32	1966-2004	1,057 (1982)	ICES 2005; WGBFAS
North Sea (NSEA)	IIIIa, IV, VIId	1963-2004	1,146 (1980)	ICES 2005; WGNSSK
Iceland (ICE)	Va	1955-2004	2,282 (1955)	ICES 2005; NWWG
Faroe Plateau (FAR)	Vb1	1961-2004	155 (1976)	ICES 2005; NWWG
W. Scotland (WSCT)	VIIa	1978-2004	54 (1980)	ICES 2005; WGNSDS
Irish Sea (ISEA)	VIIa	1968-2003	30 (1973)	ICES 2005; WGNSDS
Celtic Sea (CSEA)	VIIe-k	1971-2003	34 (1988)	ICES 2005; WGNSDS

NAFO is Northwest Atlantic Fisheries Organization. ICES is the International Commission for the Exploration of the Sea. The ICES assessment reports are at <http://www.ices.dk/iceswork/workinggroups.asp>.

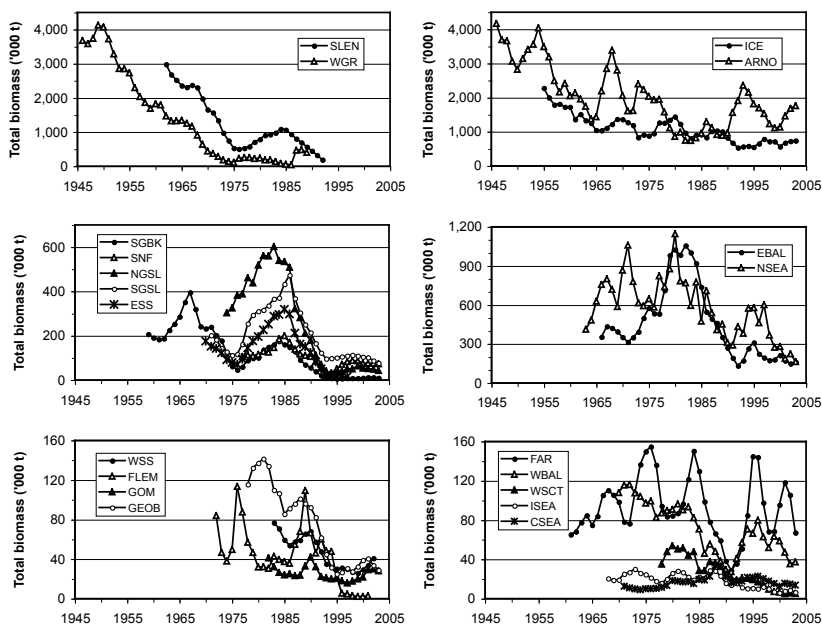


Figure 2. Total biomass (thousand t), as estimated by sequential population analysis (SPA), for cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Note differing scales on ordinate axes. Data sources as in Table 1.

of stock dynamics (Lilly 2008). The extent of decline in this stock, as deduced from research vessel catches, is considerably greater than indicated by SPAs of the early 1990s (Bishop et al. 1993), but somewhat less than indicated by the SPA used by Smedbol et al. (2002) and reported by Shelton et al. (2006).

If 1970 is used as a point of reference (Brander 2007), then all stocks except the Celtic Sea stock have declined (Fig. 2). However, there have been periods of increase and of decrease in almost all stocks, and even the Celtic Sea stock is now below its peak in the late 1980s. In addition, the longer term views available for some stocks, especially those of West Greenland and the Barents Sea, suggest that the extent of decline during the latter half of the twentieth century may actually be greater than indicated by the short-term view afforded by current assessment models.

As noted above, the declines have been more pronounced in the Northwest Atlantic than in the Northeast (Fig. 2). The West Greenland stock declined to a low level by the mid-1970s and collapsed in the early 1990s (Fig. 2; Hovgård and Wieland 2008). The Northern Labrador stock (not shown because no SPA is available) had collapsed by the late 1970s and had virtually disappeared by the late 1980s (Smedbol et al. 2002, Lilly and Murphy 2004). Stocks farther south off Atlantic Canada, from Southern Labrador–Eastern Newfoundland to the eastern Scotian Shelf, continued to be productive into the 1980s, but collapsed in the late 1980s and early 1990s (Fig. 2). In contrast, stocks in the Northeast Atlantic are currently in a variety of states, from moderately good (arcto-Norwegian, Iceland) to depressed (west of Scotland, North Sea, Baltic Sea), but none are considered to have collapsed.

Major hypotheses for changes in stock biomass

Stock biomass is influenced by the effects of fishing and climate on recruitment, individual growth, and mortality. The various factors interact, and it is often difficult to disentangle them.

Fisheries

The effect of fisheries on stock biomass

It is generally accepted that excessive fishing pressure has been the major reason for the declines in cod stocks (Myers et al. 1996, Sinclair and Murawski 1997). However, there are many reasons why fishing may have been excessive, and their relative importance may differ considerably among stocks. The reasons for overfishing include management goals that may not have been precautionary, especially in earlier years (Sinclair and Murawski 1997, Garcia and Moreno 2005), scientific overestimation of population size (Sinclair et al. 1991, Mohn 1999), the establishment of management plans that include landings in excess of scientific advice (Horwood et al. 2006, Shelton et al. 2006), and the killing of fish in excess of the amount specified in management plans. The latter includes reported overruns and non-reported catches, which may include both landings (Horwood et al. 2006) and discards (Hutchings and Ferguson 2000). A full inquiry into causes of declines and recoveries should include and distinguish among the above components. We can mention only a few examples.

The importance of unrestrained fishing is clearly demonstrated in the Northwest Atlantic, where distant-water trawling fleets caused a substantial increase in landings during the late 1950s and 1960s (Fig. 3) and contributed to a rapid decline in the biomass of several stocks during the 1960s and 1970s (Fig. 2). The declaration of 200 nautical mile fisher-

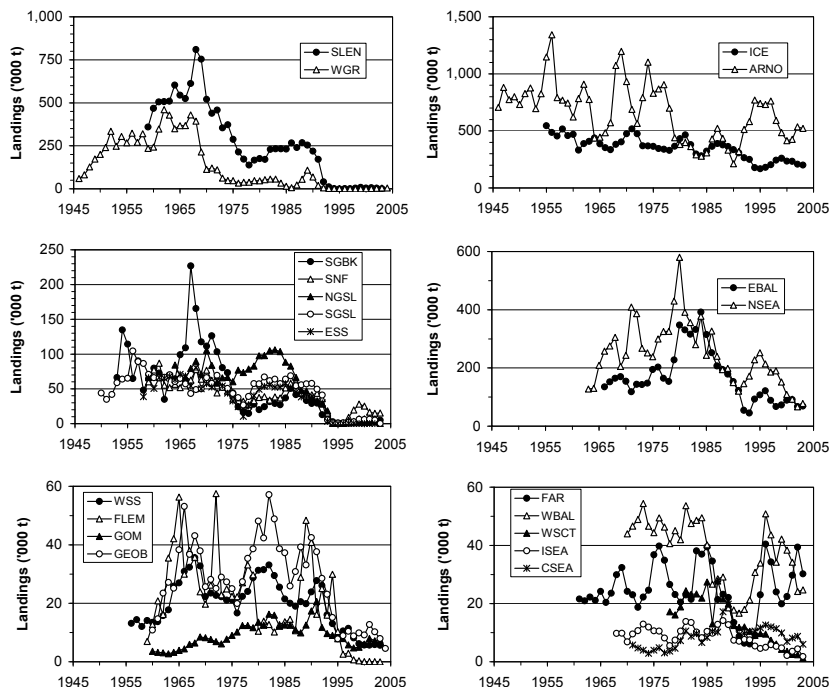


Figure 3. Landings (thousand t) from cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Note different scales on ordinate axes. Data sources as in Table 1. For Gulf of Maine (GOM), landings to 1981 are commercial only, and commercial plus recreational thereafter. For Flemish Cap (FLEM), landings from 1988 to the late 1990s include estimates that represent a large proportion of the total.

ies zones in 1977 reduced fishing mortality temporarily and contributed to recovery of many stocks, especially S. Labrador–E. Newfoundland, southern Grand Bank, southern Newfoundland, and eastern Scotian Shelf. However, most Canadian stocks declined once again, and to a greater extent, during the late 1980s and early 1990s. Some investigators (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1996) have stated that these declines during the late 1980s and early 1990s were caused entirely by fishing, and indeed SPA modeling indicates a sharp increase in fishing mortality for many of these stocks, most notably those from the eastern Scotian Shelf northward to S. Labrador–E. Newfoundland (Fig. 4). Fishing mortality tended to be chronically higher

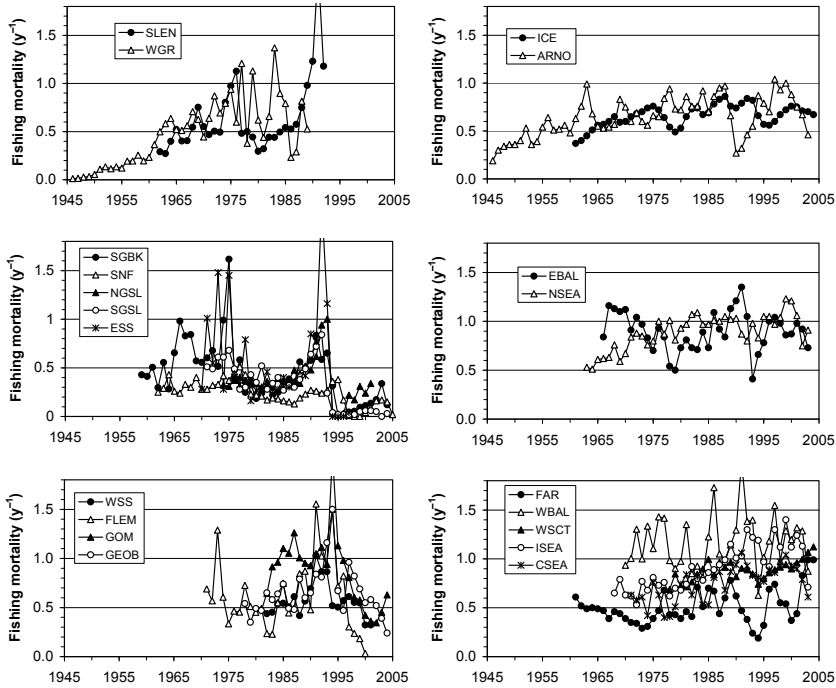


Figure 4. Fishing mortality, as estimated by sequential population analysis (SPA), for cod stocks in the Northwest Atlantic (left panels) and Northeast Atlantic (right panels). The stocks are arranged from large (top panels) to small (bottom panels). Data sources as in Table 1.

than intended (the retrospective problem as described in Sinclair et al. 1991), but the cause of the sharp rise in fishing mortality is not entirely clear. In the case of the S. Labrador–E. Newfoundland stock, there was a large and sudden downward re-evaluation of the population estimate in 1988–1989 (Baird et al. 1991) and, for socioeconomic reasons, the total allowable catch (TAC) was not adjusted downward to the full extent implied by the revised estimate, causing fishing mortality to rise rapidly (Shelton 1998). It is unclear whether this by itself can explain the collapse of the stock because reported landings have been insufficient to account for the large and rapid decline in indices of abundance from research surveys (Shelton and Lilly 2000, Lilly 2008). Additional factors that might have contributed to the collapse are discussed below.

If fishing were the only, or major, cause of the declines, then cessation of fishing might be expected to halt and then reverse the declines

(Myers et al. 1995). Moratoria on directed fishing were indeed instituted for S. Labrador–E. Newfoundland cod in 1992, for all other stocks adjacent to Canada as far south as the eastern Scotian Shelf in 1993, for southern Grand Bank cod in 1994, and for Flemish Cap cod in 1999. The effects of these moratoria were variable but generally much less positive than had been hoped (Rice et al. 2003). The S. Labrador–E. Newfoundland and eastern Scotian Shelf stocks continued to decline after imposition of the moratoria, and have shown no signs of recovery even though directed fisheries have remained closed (except for coastal fisheries that targeted inshore populations of the S. Labrador–E. Newfoundland stock during some years). The fishery on the southern Grand Bank cod stock has also remained closed, but there is evidence that recovery has been impeded by bycatch in fisheries directed at other species (Shelton and Morgan 2005). The Flemish Cap stock has shown no sign of recovery. The two stocks in the Gulf of St. Lawrence recovered slightly, but small directed fisheries during most years since 1998 have reversed most of the gains. Local inshore populations off eastern Newfoundland (the coastal region of the S. Labrador–E. Newfoundland stock) also increased, but directed fisheries during 1998–2002 contributed to a substantial decline (Lilly et al. 2005). Only the southern Newfoundland stock has experienced substantial recovery and has remained open to directed fishing since being reopened in 1997. However, even that stock has been declining recently. The reopening of directed fisheries on the two Gulf of St. Lawrence stocks and the inshore area of the S. Labrador–E. Newfoundland stock are examples of instances wherein short-term socioeconomic concerns and statements by fish harvesters regarding stock status have taken precedence over the information provided by a formal scientific stock assessment process.

The contrast between the rapid rebuilding of Canadian stocks in the 1970s and early 1980s and the virtual absence of recoveries during the late 1990s and early 2000s remains only partly explained (Rice et al. 2003). The directed and bycatch fisheries of the 1990s and 2000s are certainly part of the reason (Shelton et al. 2006), but other factors appear to have contributed to lower productivity.

Other consequences of fishing

Fishing may affect populations in several additional ways. Mean age and age diversity of spawners has declined in many stocks (Marteinsdottir et al. 2005), and this has been found to affect recruitment in some stocks. For example, decline in age diversity has been associated with low recruitment in Icelandic cod (Marteinsdottir and Thorarinsson 1998). However, such an effect was not found in southern Gulf of St. Lawrence cod (Swain and Chouinard 2000). The decline in mean age and age diversity of spawners in arcto-Norwegian cod has resulted in recruitment becoming more strongly influenced by climate variability

(Ottersen et al. 2006). Fishing may cause changes in life-history traits, such as growth rate and age and size at maturation (see below). Fishing stocks down to low levels may also affect their viability because of behavioral problems, such as increased difficulty in finding a mate and breakdown of migration patterns or social structures (Allee effects; Frank and Brickman 2000). There could also be depensation associated with predation, as discussed below.

Climate variability and change

Cod stocks may respond to decadal-scale climate changes. For example, the warming of much of the northern North Atlantic during the 1920s and 1930s resulted in a general northward expansion of many fish species, including cod (Rose 2005, Drinkwater 2006). The most conspicuous change was the increased abundance and northward expansion of cod at West Greenland (Hovgård and Wieland 2008), but there was also expansion of cod farther to the north and east in the Barents Sea and increased use of northern spawning areas at both Iceland and the Norwegian coast.

Important changes were also associated with the increasingly positive (high) phase of the North Atlantic Oscillation (NAO) from the 1960s to the 1990s. During this period, the positive phase tended to result in decreased air and sea temperatures and increased ice cover in the Northwest Atlantic from the Labrador coast to the eastern Scotian Shelf, and contributed in several ways to a reduction in productivity of cod stocks in that region (Drinkwater 2002). In contrast, the intensification of the positive phase of the NAO led to increased inflow of warm Atlantic water into the Barents Sea, promoting recruitment to the arcto-Norwegian cod stock (Ottersen and Stenseth 2001). North-south differences in the impact of the NAO on cod recruitment have also been found. During a positive NAO phase, recruitment tends to be lower than normal in the southernmost stocks on both sides of the Atlantic and higher in the northernmost stocks (and vice versa for negative phase) (Brander and Mohn 2004, Stige et al. 2006).

Finally, the North Atlantic has been warming during the past decade (ICES 2006c). Although higher temperatures are generally expected to be beneficial for cod toward the northern limits of cod distribution (Planque and Frédou 1999, Drinkwater 2005), there has been little response to date off eastern Canada (Shelton et al. 2006). For cod populations toward the southern limit of cod distribution, the warming may prove to have negative effects (Planque and Frédou 1999, Drinkwater 2005).

Stock demographics and life-history traits

Recruitment

Much of the variability in heavily exploited cod populations is due to changes in recruitment. This is particularly evident when populations increase. For example, the abundance of cod at Greenland has been strongly dependent on the arrival of larval cod from Iceland (Drinkwater 2006, Hovgård and Wieland 2008). The increase in abundance of North Sea cod during the “gadoid outburst” of the 1960s and 1970s was due to an increase in average recruitment (Hislop 1996, Heath and Brander 2001).

Many hypotheses have been proposed to explain variability in recruitment to specific cod stocks (ICES 2005). The spawning potential of the parent population is generally assumed to be of major importance, but many factors affect the survival of progeny, such that there may be considerable among-year variability in the number of recruits per unit of spawning biomass. A high survival of progeny (recruits per unit of spawning biomass) contributed to the increase in several Canadian cod stocks in the late 1970s and early 1980s (Sinclair 1996, Chouinard et al. 2003), whereas a low (or lower) survival contributed to the decline of some of the same stocks in the late 1980s and early 1990s and their weak recovery during the late 1990s and 2000s (Shelton et al. 2006). The mechanisms by which pre-recruit survival is affected involve many aspects of the physical and biotic environment. Physical mechanisms include annual variability in the transport of the zooplanktonic food for cod larvae into the Barents Sea and North Sea (Sundby 2000) and the replenishment of salinity and oxygen in the Baltic Sea by episodic inflow of water from the Kattegat and the North Sea (Köster et al. 2005). Some examples involving feeding and predation are discussed below.

Growth

Changes in recruitment and fishing mortality have received most of the attention regarding changes in stock size, but variability in individual growth may also be important. Sinclair (1996) noted that the gradual reduction in weight-at-age from the late 1970s to the early 1990s has had a notable effect on the biomass of several stocks off Canada (particularly S. Labrador–E. Newfoundland, northern and southern Gulf of St. Lawrence, and eastern Scotian Shelf). Brander (2007) examined changes in total biomass in 15 stocks from across the Atlantic, and found that 14 have declined since 1970. In 10 of these, the periods of decline were preceded by or coincided with declines in mean weight-at-age. For the ten stocks experiencing periods of increasing total biomass, all increases were accompanied by increasing weight-at-age.

Changes in growth affect productivity and thus the biomass that can be harvested sustainably for a given fishing mortality. In addition,

Drinkwater (2002) and Brander (2007) suggested that, because TACs are in terms of weights, declines in weights-at-age should have resulted in increased numbers of fish caught per unit of quota. It is not clear whether this mechanism has played a role in Canadian stocks, because the catch predictions have generally been based on the average weight-at-age during recent years, and should therefore be close to the actual value (unless weight-at-age dropped suddenly and substantially from one year to the next). It might be of interest to investigate whether such a mechanism has contributed to the rise in fishing mortality in several Canadian stocks during the late 1980s and early 1990s.

Changes in size-at-age within a stock may result from several factors, including changes in temperature, stock size, prey abundance (see below), and size-selective fishing (Sinclair et al. 2002a,b). With respect to temperature, among-stock comparisons have shown that growth rate (Brander 1995), condition (Rätz and Lloret 2003), and overall productivity (Dutil and Brander 2003) are higher in stocks that live at higher temperatures. In addition, evidence from experiments and in the field shows that the effect of temperature change is progressively greater at lower temperatures (Brander 2007). Thus, the cooling of the 1980s and early 1990s off eastern Canada from the eastern Scotian Shelf northward may have had a particularly strong influence on cod in that area because they were already living in a relatively cold environment. Nevertheless, the large changes in size-at-age of cod in the southern Gulf of St. Lawrence from 1971 to 1998 appear to be most strongly related to changes in size-selective mortality, followed by effects of density-dependent growth, with only relatively minor variation attributed to changes in the temperature of the water occupied by the cod (Sinclair et al. 2002b).

A persistently low growth rate has been an important contributor to the continuing low productivity of several stocks off Canada (Shelton et al. 2006). This is particularly the case for the stock in the southern Gulf of St. Lawrence (Chouinard et al. 2003), and Swain et al. (2007) provide evidence that this may have been caused by genetic change in response to size-selective fishing.

Maturity

Age- and size-at-maturity have declined in many stocks (Marteinsdottir and Begg 2002). An examination of probabilistic maturation reaction norms (Heino et al. 2002) provides evidence for a genetic change, most likely in response to fishing, in all stocks investigated, viz. Georges Bank and Gulf of Maine (Barot et al. 2004), S. Labrador–E. Newfoundland, southern Newfoundland and southern Grand Bank (Olsen et al. 2005), and arcto-Norwegian (Heino et al. 2002). Maturing early gives a selective advantage under most high mortality regimes, because only fish that mature and reproduce before being caught will pass their genes to the

next generation. Reversion to older age-at-maturity and larger size-at-maturity when mortality is reduced may be slow if late maturation does not offer a strong selective advantage (Law 2000).

In the context of recovery from low population size, Hutchings (2005) conducted simulations to explore the consequences of a reduction in age-at-maturity, coupled with additional factors such as reduced reproductive success in first-time spawners and increased mortality upon attainment of maturity. He found that a reduction in age-at-maturity might reduce annual population growth, and concluded that fishing-induced changes in life-history traits might in themselves impede recovery.

Natural mortality

The importance of changes in natural mortality to the dynamics of cod stocks has received increased emphasis with the recognition that mortality remained high in several depressed stocks off eastern Canada after directed fishing was stopped, and that increased natural mortality slowed stock recovery (Shelton et al. 2006). Several analyses (e.g., Sinclair 2001) demonstrated that natural mortality started to increase well before the fisheries were closed. For the cod stock in the southern Gulf of St. Lawrence, analyses suggest that the increase in natural mortality played a role in the collapse of the stock (Chouinard et al. 2005), and this may be true for several other stocks as well.

A series of publications during the mid-1990s (Hutchings and Myers 1994, Myers and Cadigan 1995, Hutchings 1996, Myers et al. 1996) stated that there was no evidence of an increase in natural mortality in the S. Labrador–E. Newfoundland stock and other Canadian cod stocks during the period of collapse. It was only after data had accumulated for several additional years that analyses started to provide evidence that natural mortality had indeed increased, and such an increase was then incorporated into SPA models for the stocks in the northern (Fréchet et al. 2005) and southern (Chouinard et al. 2006) Gulf of St. Lawrence and the stock on the eastern Scotian Shelf (Mohn et al. 1998). The use of SPAs for the S. Labrador–E. Newfoundland stock as a whole was discontinued during the early 1990s, but exploration of these models demonstrated that reported landings were insufficient to account for the large and rapid decline in indices of abundance from research surveys (Shelton and Lilly 2000, Lilly 2008). The “missing fish” could be attributed to increased levels of unreported landings or discards, but might also be the result of increased natural mortality. More recently, tagging studies have provided evidence of elevated natural mortality in inshore populations along the east coast of Newfoundland (Lilly et al. 2005).

Biotic factors affecting stock biomass

Prey

Changes in the abundance or availability of prey may have consequences for growth (and condition), recruitment, and mortality of the predators. Such influences are more commonly detected in ecosystems that have relatively few prey species, such as the Baltic Sea and the arcto-boreal areas.

Capelin abundance has been positively correlated with growth rate in Icelandic cod (Stefánsson et al. 1998) and arcto-Norwegian cod (Mehl and Sunnanå 1991), and with somatic condition and liver reserves of arcto-Norwegian cod (Yaragina and Marshall 2000). For S. Labrador–E. Newfoundland cod, Krohn et al. (1997) reported that capelin biomass explained some of the variability in cod growth and condition, but other studies did not find a significant relationship (ICES 2006b, p. 89). In contrast to the positive association often seen elsewhere, the condition of cod and other groundfish species on the eastern Scotian Shelf declined significantly (Choi et al. 2004) at the same time as the biomass of pelagics increased. Bundy and Fanning (2005) hypothesized that the poor condition observed in small cod is due to competition with increased populations of planktivorous fish, and proposed that cod that are in poor condition when small may remain that way when they become larger.

A decline in condition (or liver index) might affect spawning potential of cod stocks by decreasing the likelihood of maturing (Martensdottir and Begg 2002), increasing the incidence of skipped spawning (Rideout et al. 2005, Jørgensen et al. 2006) and reducing the reproductive output of those fish that do spawn (Lambert and Dutil 2000).

In the absence of findings of dead or moribund fish, the question of whether a decline in cod condition has contributed to an increase in natural mortality (other than predation) is difficult to address. Nevertheless, fish exhibiting critically low condition for survival (according to the value determined to be critical in a laboratory setting) were found in the northern and southern Gulf of St. Lawrence (Lambert and Dutil 1997, Schwalme and Chouinard 1999) during the early to mid-1990s. Dutil and Lambert (2000) concluded that natural mortality from poor condition contributed to lower production of the northern Gulf of St. Lawrence cod. It is not clear whether the poor condition was related to a decline in abundance of prey, but it has been hypothesized that cooling caused a shortening of the feeding season (Castonguay et al. 1999). The decline in condition of eastern Scotian Shelf cod is not related to the abundance of pelagic prey, because the historically important prey species increased following the cod collapse (see above). For S. Labrador–E. Newfoundland cod, it was hypothesized that the collapse might be due in part to an increase in stress associated with a change

in abundance and availability of capelin (Atkinson and Bennett 1994), but data from the appropriate times and locations may be insufficient to test this hypothesis (Lilly 2001). With respect to the lack of recovery in the offshore portion of the S. Labrador–E. Newfoundland stock, Rose and O'Driscoll (2002) stated that the high mortality experienced by cod since the collapse is due to poor condition, which in turn is due to low capelin availability (but see Lilly et al. 2005).

The abundance of forage species might also affect cod through secondary links in food webs. For example, it has been hypothesized that when forage species such as capelin are in low abundance, then predators such as harp seals (Nilssen et al. 2000) may feed to a greater extent on cod. Also, cannibalism might increase within a cod population when prey abundance is low, and this might reduce year-class strength. For example, the incidence of cannibalism in arcto-Norwegian cod appears to increase when capelin biomass is low (Hamre 2003, ICES 2006a).

Planktivorous forage fish might affect cod by preying on, or competing with, its early life-history stages (eggs, larvae and perhaps pelagic juveniles). A negative relationship between the biomass of pelagic fish (herring and mackerel) and the number of recruits per unit of spawning biomass of cod has been shown for the southern Gulf of St. Lawrence (Swain and Sinclair 2000). High values of recruits per unit of spawning biomass from the mid-1970s to the early 1980s coincided with a period during which pelagic biomass had been reduced by overfishing. A variant of this mechanism is the "cultivator effect": a large predator may protect its offspring by preying on species that are their potential predators and competitors. If the predator becomes less abundant, its prey becomes more abundant, through released predation, and then keeps the predator under control at a low level by preying on or competing with its early life-history stages. Such a mechanism has been hypothesized for cod and its planktivorous fish prey in the Baltic Sea (Köster and Möllmann 2000) and on the eastern Scotian Shelf (Bundy and Fanning 2005).

Predators

Predation is an important component of natural mortality, especially for smaller cod, as has been illustrated by numerous diet studies and multispecies models. An important question is whether natural mortality varies over time, and whether such variability contributes to large changes in stock abundance.

As noted above, natural mortality evidently increased in several Canadian stocks during the 1980s and has remained high. The causes remain unclear and contentious. Numerous studies have discussed the possibility that predation by (gray and/or harp) seals is an important component of the high mortality in the eastern Scotian Shelf stock (Fu et al. 2001, Bundy and Fanning 2005), in the southern and northern Gulf

of St. Lawrence stocks (Chouinard et al. 2005, Fréchet et al. 2005) and in the S. Labrador–E. Newfoundland stock (Lilly et al. 2005). Formal cod stock assessment meetings within Canada have concluded that predation by seals has contributed to recovery of these stocks being slow or nonexistent (Rice et al. 2003).

One of the paradoxes associated with these analyses is that elevated mortality appears in not only juvenile cod but also adult cod, whereas diet data generally reveal seal feeding only on small cod (Hammill and Stenson 2000). It has been suggested by some (e.g., Chouinard et al. 2005) that the high mortality of adult cod might be a consequence of belly-feeding (a manner of feeding whereby the seal takes a bite from the cod's belly, leaving the head and muscle mass). Such feeding by seals is difficult to detect by visual examination of stomach contents or scats because there are no hard parts involved. However, belly-feeding by harp seals on cod has been observed in eastern Newfoundland (Lilly and Murphy 2004).

The heightened attention to the role of seals and other marine mammals in the dynamics of cod stocks off Canada is partly due to opposing population trends. Many species of marine mammals were heavily exploited for centuries and consequently declined to low numbers, but some have increased during the recent 2–3 decades under more restrictive management measures. In the Northwest Atlantic, this is particularly the case for harp seals (Hammill and Stenson 2005) and gray seals (Trzcinski et al. 2005). In contrast, exploitation of cod has increased in recent decades, and many stocks are at all-time lows. Seals (and other marine mammals) do not have a strong dependency on cod, their major prey usually being pelagic species of fish and squid. However, if these predators continue to eat some cod even if cod abundance is low, then they may contribute toward keeping the cod in a “predator pit” (Shelton and Healey 1999). Marine mammals may also compete with cod for prey resources such as capelin and sand lance, thus affecting cod growth and condition.

Loss and re-establishment of spawning populations

It has long been recognized that Atlantic cod has a rich population structure, with many of the unit stocks identified for management purposes (Fig. 1; Table 1) consisting of several substocks or metapopulations (Templeman 1962). Ames (2004) provides evidence that some of this substock structure may have disappeared, or have been reduced, even before the initiation of scientific study of the Atlantic cod resources. The existence of metapopulation structure has been supported and amplified by recent studies using advanced techniques in fields such as genetics (Ruzzante et al. 1999), otolith chemistry (Jónsdóttir et al.

2006), and tagging (Wright et al. 2006). The view of stock dynamics afforded by SPA (Fig. 2) provides considerable reason for concern about the viability of "unit stocks," but there are additional concerns related to maintaining population diversity within the stocks (Frank and Brickman 2000, Smedbol and Stephenson 2001). Some components may be more susceptible than others to overexploitation because they are smaller, less productive, or more accessible for harvesting. The extent to which among-component differences in recruitment, growth, and mortality have contributed to the overall decline in unit stocks is by no means clear. However, there are examples of different population trajectories within the established unit stocks. The S. Labrador–E. Newfoundland stock declined first in the north (deYoung and Rose 1993, Lilly 1994) and the recent decline in North Sea cod has been more pronounced in the south (Horwood et al. 2006).

An important question for management is whether areas where stocks or stock components have been depleted can be repopulated by cod from adjacent areas. Obviously, colonization of suitable areas has happened over the scale of millennia, but evidence of recolonization of vacated areas or supplementation of depleted areas during recent times is less clear. Much of the increase in the cod at West Greenland during the 1920s and 1930s was due to eggs and larvae imported by currents from Iceland (Buch et al. 1994), but it remains uncertain whether the fish from Iceland established self-supporting spawning populations at West Greenland, as stated by Anisimov et al. (2007), or depended on the inflow of new recruits from Iceland. Along the eastern Skagerrak coast, where local spawning aggregations have been depleted, juvenile cod may still occur in high numbers in some years, but most are recruited from offshore spawning areas, mainly in the North Sea, and they return to offshore areas instead of spawning locally along the coast (Svedäng and Svenson 2006). For the S. Labrador–E. Newfoundland stock, there is concern that fishing on inshore populations will lessen the likelihood that those populations will expand to offshore waters and establish spawning groups there (Lilly et al. 2005). However, Beacham et al. (2002) contend that the population substructure that has been demonstrated between most inshore and offshore areas indicates a low likelihood that inshore-spawning cod will contribute to offshore recovery. In addition, Ruzzante et al. (2001) found that the geographic pattern of genetic differentiation in the offshore remained stable from the mid-1960s (pre-collapse) to the mid-1990s (post-collapse), from which they inferred that if recovery eventually occurs, it will likely be through *in situ* population re-growth rather than by immigration.

Concluding remarks

We provide examples of the insight that may be derived from among-stock comparisons. However, there is much opportunity for additional study. For example, the stocks off eastern Canada differ with respect to the extent of collapse, degree of recovery, and relative importance of the various factors contributing to low productivity since the collapse. These differences exist over short distances, and could provide the contrast required for more detailed investigation. Another example of strong contrast is the divergent histories of arcto-boreal stocks on either side of the North Atlantic. What have been the relative roles of fisheries and climate variability (especially with reference to the North Atlantic Oscillation) in the collapse of the S. Labrador–E. Newfoundland stock and the persistence of the arcto-Norwegian stock?

A general conclusion from the experience off eastern Canada is that fisheries scientists and managers may have limited ability to “rebuild” to previous levels any cod stocks that might decline to very low levels. Simply turning off directed fishing may be insufficient to promote recovery. Bycatch in fisheries directed at other species in conjunction with various natural phenomena, including depensation due to predation and altered life-history traits, may constrain such stocks at low abundance for considerable periods.

The effects of fishing and climate variability interact. Stocks may become more sensitive to the effects of fishing when adverse climate conditions reduce productivity (reduced recruitment and growth; increased natural mortality) and more sensitive to climate when fishing has caused changes in population processes (growth, maturation) and demographic properties (age structure and geographic sub-structure). Some life-history traits, especially growth and maturation, can be monitored by sampling commercial and research catches and may give timely indications of changes in productivity. In order to develop their routine use in assessing risk of collapse under different fisheries management strategies, indicators of possible change in productivity, such as weight-at-age, somatic condition, liver index and maturation reaction norm, should be investigated using tropho-dynamic, life-history, and risk-assessment models.

Acknowledgments

We thank L. O’Brien for providing data, H. Hovgård and A. Sinclair for their insight regarding certain issues, and J. Ianelli, M.J. Morgan, J. Brattey, S. Cadrin, and an anonymous reviewer for their helpful comments on an early draft of this manuscript. The authors were participants in the ICES/GLOBEC workshop on “The Decline and Recovery of Cod Stocks throughout the North Atlantic, Including Tropho-Dynamic Effects” (May 2006). This paper is a contribution to the ICES/GLOBEC Cod and Climate Change Program.

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